SUPPLEMENTARY NOTES.

SALYAVATINÆ.

Lisarda inornata.

Acanthaspis inornata, Walk. Cat. Het. vii. p. 175. n. 51 (1873). Lisarda pallidispina, Stål, En. Hem. iv. p. 83 (1874).

A CANTHASPINE:

Genus PASIRA.

Pasira perpusilla.

Reduvius perpusillus, Walk. Cat. Het. vii. p. 196. n. 50 (1873).

Pasira pusilla.

Reduvius pusillus, Walk. Cat. Het. vii. p. 193. n. 43 (1873).

Clavus, base of corium, a linear spot near centre of apical margin of corium, spots to connexivum, and extreme apices of anterior femora obscure brownish ochraceous.

XLII.—Notes on the Classification of Teleostean Fishes.— IV. On the Systematic Position of the Pleuronectidæ. By G. A. BOULENGER, F.R.S.

In the classification of Cuvier, at the beginning of the last century, the presence or absence of spines in the dorsal fin was regarded as of so great importance in the Teleostean fishes that they were primarily divided into Acanthopterygians and Malacopterygians. According to the presence or absence and the position of the ventral or pelvic fins, the latter division was again split up into three groups-Abdominals, Subbrachials, and Apodes. The Gadoids and Pleuronectids were thus brought together as Subbrachial Malacopterygians. When Johannes Müller took up the condition of the airbladder as a basis for the establishment of higher groups, these Subbrachial Malacopterygians were removed from the Abdominals or Physostomes and placed nearer the Acanthopterygians, but remained associated under the name Anacanthini. And so they have been in most classifications, even modern text-books teaching us that flat-fishes are only modified asymmetrical Gadoids. But any one who will carefully compare the anatomical structure of the principal members of these two families cannot fail to recognize the absurdity of

such a conception. The Anacanthini, as defined by Müller, are a purely artificial group, for the recognition of which not even the excuse of external similarity can be adduced.

A step in the right direction had already been made by Cope in 1871 *, followed later by Gill and by Jordan, in separating the flat-fishes as a suborder under the Dumerilian name of Heterosomata, but merely on account of the asymmetry of the skull, and, to quote from the latter author +, persisting to consider the nearest relationship of this subor-ler to be "probably with the Gadidæ, although the developed pseudobranchiæ and the thoracic fins indicate an early differentiation from the Anacanthine fishes."

Objections to this view were raised by J. T. Cunningham in 1897 ‡, who observed :-- "It is a remarkable fact that although the Pleuronectidæ and Gadidæ have generally been considered to be so similar that they have been placed in the same order Anacanthini, the structure and development of the tail described above [heterocercy] occur in the flat-fish, but are entirely wanting in the Gadidæ. In the latter the tail is permanently diphycercal, it is composed of dorsal and ventral rays which are equal in number and size, and, in fact, closely resemble the tail of the extinct Coelacanthidæ. There can be little doubt that even if the Gadidæ cannot be directly derived from the latter family, they are descended from Crossopterygian Ganoids with diphycercal tails, and have never passed through a heterocercal condition §. Although the structure of the tail in the Gadidæ was briefly and correctly described by Alexander Agassiz in his paper on the development of the tail, he did not attach sufficient importance to it, believing that a very slight apparent up-bending of the termination of the notochord showed the essential similarity in the development of this type of tail with that seen in other Teleosteans. The proper classification of the Anacanthini is yet to be worked out, but there can be no doubt that the Gadidæ and Pleuronectidæ, instead of being closely allied, are very remote from each other in structure and descent."

The latter conclusion had already been reached by Agassiz from the study of fossils. On p. 260 of the fourth volume of his ' Poissons fossiles,' dealing with the curious extinct genus Macrostoma (= Amphistius), to which I shall have occasion to refer presently, he expresses the opinion that "L'ensemble

- * Trans. Amer. Philos. Soc. (2) xiv. 1871, p. 458.
- † 'Fishes of N. America,' iii. p. 2602 (1898).
 ‡ 'Science Progress,' (2) i. p. 498.
- § See my remarks on this subject, further on.

bizarre de caractères que présente ce genre me paraît une confirmation éclatante du rapprochement que j'ai fait des Pleuronectes et des Chétodontes, et si l'on fait abstraction des rayons épineux de ces derniers, ou plutôt si l'on considère le peu d'importance que mérite ce caractère dans une famille qui compte des genres conformés comme les *Platax* et les *Psettus*, on ne méconnaîtra pas leur intime affinité. Q t'on ne m'objecte pas la conformation bizarre et irrégulière de la tête des Pleuronectes; car où qu'on les range, ils se distingueront toujours par là de tous les poissons connus."

Somewhat the same suggestion as that of Agassiz was again incidentally made by E. W. L. Holt in 1894 * :--"Messrs. Cunningham and MacMunn find a difficulty in accepting reversion or atavism as an explanation of the ambicolorate condition, in that the hypothetical vertically swimming ancestor of the flat-fish must have had an unpigmented white or silvery ventral surface, as other symmetrical fishes have, whereas completely ambicolorate flat-fish are uniformly pigmented all over. The difficulty certainly arises if we assume that the ancestor really was paler on the ventral region than elsewhere; but is it not equally reasonable to assume a stage of evolution in which the fish resembled such forms as *Platax* or *Dascyllus*, to take instances from families widely separated from each other by systematists? Both forms have high compressed bodies, and in some species, at any rate, of both genera the ventral region is as deeply pigmented as the dorsal. Even in the John Dory (Zeus taber), in which the ventral abdominal region is flattened, it is nevertheless rather darkly pigmented, and to me it certainly seems more probable that the Pleuronectidæ of the present day began to take on their asymmetrical characters as compressed and uniformly coloured forms than in the condition of ordinary round fish."

Merely for the sake of completeness would I allude to the suggestion made by Gill in 1887 † :--- "I am half inclined to think that the Heterosomatous fishes may have branched off from the original stock, or progenitors of the Tæniosomous fishes [Trachypteridæ]. I shall investigate the subject when I can get the requisite material." Dr. Gill has not published the reasons which made him incline towards such a conclusion, and the position in which he has left the Pleuronectids in his latest classification ‡, with the Anacanthini between them and the Trachypterids, seems to show that the idea of

* P. Z. S. 1894, p. 438.

† Amer. Natur. xxi. p. 86.

‡ Mem. Nat. Acad. Washington, vi. 1893, p. 137.

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any very close relationship between these two aberrant groups has been abandoned by him *.

In spite of the absence of spines in the fins, the Gadoids offer a combination of characters—closed air-bladder, jugular ventral fins, reduced parietal bones, maxillary excluded from the border of the mouth—which, taken together, indicate descent from the Acanthopterygians, and not from the lower Teleosteans, a conclusion further supported by their relationship to the Blenniids and Trachinids. This being admitted, it follows that the characters which serve to define them as a group are the result of specialization, not primitive. These characters are :—

1. The diphycercal or isocercal † termination of the vertebral column. This has often been regarded as a primitive character; but if we accept, as I do, the conclusions of Dollo in his remarkable discussion of the Dipneusti t, we cannot hesitate to lay down as an axiom that all Teleosteans are originally descended from heterocercal forms. But the caudal fin may become reduced or disappear, as in the series Mormyrops-Gymnarchus, Urenchelys-Muræna, Thyrsites-Trichiurus, Pleuronectes-Cynoglossus, to mention only examples in which the direction of the line of evolution does not seem open to controversy; and if it should reappear, it cannot be again in the specially modified condition known as homocercy. Such a form of secondary caudal fin is exemplified among the Crossopterygians by the Cœlacanthidæ §. I have reason to believe that the Gadoids must have been derived from such a group as the Berycidæ, through forms of which the Macruridæ, with thoracic ventral fins composed of 7 to 12 rays, are the nearest known examples, and in which the caudal fin had entirely vanished. I regard the isocercal condition of the Gadidæ as the result of the formation of a new caudal fin, the homocercal extremity of the vertebral column having been lost by the direct ancestors of these fishes.

2. The relations of the bones supporting the pectoral fin, which differ considerably from those of the earlier Acanthopterygians. The scapular bone is imperforate and the fenestra is situated between it and the coracoid. Of the basalia or

- It is not improbable that the Trachypteridæ have branched off from the hypothecial primitive Acanthopterygians out of which the Berycidæ, Zeidæ, and Macruridæ may be derived.
- + For definitions of these terms, cf. Boulenger, Poiss. Bass. du Congo, p. 7 (1901).
 - t Mém. Soc. Belge Géol. ix. 1895, p. 79.

§ *Cf.* Bashford Dean, 'Fishes Living and Fossil,' p. 153, figs. 155 and 156 (1895).

pterygials, two or three are in contact with the coracoid and one or two with the scapula, this being the reverse of what obtains in the Berycidæ and most Acanthopterygians.

3. Absence of pseudobranchiæ.

If we now compare the Pleuronectidæ to the Gadoids, we find that in these three characters they differ from them and agree with the majority of the Acanthopterygians, especially with those which, geologically and morphologically speaking, may be termed the oldest. The tail, whenever a caudal fin is well developed, belongs to the homocercal type (heterocercal in the embryo), with comparatively few rays (20 or less). The pectoral fin, in its fullest development, is supported by four pterygials, of which three are attached to the scapula and one to the coracoid, and the fenestra is in the scapular bone. Pseudobranchiæ are present.

From a consideration of these characters alone, the Pleuronectidæ cannot be held to have been derived from the Gadoids, but their ancestors must be sought for among more primitive Acanthopterygians. Bearing in mind Holt's suggestion quoted above, I have proceeded to make a search among the deep-bodied, strongly compressed types, such as the so-called Squamipinnes and some of the Scombriformes. I may mention that in seeking for extinct allies of the Zeidæ I had already arrived at the conclusion that a form placed among the Carangidæ by Woodward *, Amphistium, agreed very closely with them in the structure of the vertebral column, notwithstanding the lower number of vertebræ (10+14); its caudal fin, quite similar to that of the Zeidæ, precluded its reference to the Carangidae, and a careful examination of one of the specimens preserved in the British Museum, kindly placed at my disposal for study by Dr. A. S. Woodward, convinced me that as many as eight branched rays in addition to a spine are borne by the pelvic bone-this, of course, affording a confirmation of the supposed affinity with the Zeidæ. The latter differ from all other Acanthopterygians, except the Berycidæ, Macruridæ, and various Gadidæ, in having more than five (6 to 8) articulated rays to the ventral fin-an important character, indicative of descent from a lowly type, for I am not disposed to admit that the number of rays on one bony support having once been reduced can again become multiplied. We know, in the evolution of the dorsal and anal fins, that the exoskeletal rays, having first been in excess of their endoskeletal supports (interspinous bones), became reduced so as to correspond with them in

* Cat. Foss. Fish. iv. p. 434 (1901).

number; and there is no example of their having again increased in number except concurrently with a multiplication of their supports.

The Zeidæ or Cyttidæ, comprising the genera Zeus, Zenion, and Cyttus, to which I would add the little-known Grammicolepis, described by Poey and by Shufeldt * from a single specimen, have been placed by some authors near the Chætodontidæ, by others with the Scombriformes or with the Beryeiformes. They form a perfectly natural family, which may be defined as follows:--

Acanthopterygians without subocular shelf or suborbital stay for the præoperculum, with double basis cranii †, well developed entopterygoid, and strongly protractile præmaxillaries. Two nostrils on each side. Gill-membranes free from isthmus; 7 or 8 branchiostegal rays; gills 31; pseudobranchiæ well developed. Lower pharyngeal bones separated. Vertebræ 30 to 46, the anterior with sessile ribs, the posterior præcaudals with long neural spines bent forwards and with transverse processes directed downwards, forming hæmal arches and bearing the ribs at their extremity; epipleurals much reduced or absent; hypural large, without the basal spine present in most Perciformes and all Scombriformes and Percecoces, bearing fewer than 20 rays. Dorsal and anal fins elongate, the former with a distinct spinous portion, the latter with 1 to 4 spines detached from the soft portion. Pectoral fin supported by four pterygials, of which three are in contact with the perforated scapular bone; posttemporal forked and solidly attached to the skull. Ventral fin with 1 spine and 6 to 8 soft rays.

The family which I propose to name Amphistiidæ, with the single genus Amphistium, Ag. (Macrostoma, Ag.), from the Upper Eccene, agrees with the Zeidæ in all characters that can be ascertained on the preserved remains, except that the vertebræ are fewer (24), the spines of the vertical fins are reduced to a few adnate to and continuous with the series of soft rays, and the scales are more normal and imbricate.

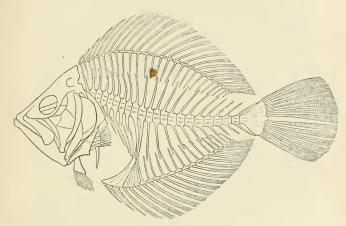
Now, as already pointed out by Agassiz, these Amphistiids, provided they be possessed of the last half-gill absent in the Zeidæ, and this is a character which unfortunately cannot be ascertained on the fossils, appear to realize in every respect the prototype of the Pleuronectidæ before they had assumed

^{*} Journ. of Morphol. ii. 1888, p. 271.

[†] I am unable to confirm the statement made by Starks (Proc. U.S. Nat. Mus. xxi. 1898, p. 470), that the basisphenoid is absent and that the parietals unite in front of the supracecipital.

Classification of Teleostean Fishes.

the asymmetry which characterizes them as a group. I am fully convinced that if they do not actually form part of the ancestral group out of which the flat-fishes were evolved, they are very nearly related to them; and it follows that the Zeidæ, of which our familiar John Dory is the best-known representative, are the nearest known living allies of the Pleuronectidæ. The number of vertebræ in *Amphistium* is



Restoration of Amphistium paradoxum, Ag., from the Upper Eocene.

rather in favour of than against such a view, since the least specialized of living Pleuronectidæ, *Psettodes*^{*}, agrees with it in this respect, all other forms of which the skeleton is known having 28 or more. Although it is perfectly true that in a general way the number of vertebræ has become reduced in the course of evolution, this law certainly does not apply to the particular groups, as seems to me proved by such series of forms as we know in the Siluridæ, Scombriformes, and especially in this instance, where the increased number is evidently related to the undulatory swimming movements of these fishes.

* In which the eye of the blind side is not lateral, but on the dorsal surface of the head, the dorsal fin does not extend on the head, the mouth is large and symmetrical, and the pelvic bones and fins are placed as in a normal Perciform.

D. S. Jordan regarded a high number of vertebræ, other things being equal, as indicative of generalization, and even thought the Pleuronectidæ afforded support to this view. Not aware of the state of things in the Hippoglossine Psettodes, he wrote # :-- " Thus in the comparatively primitive subfamily of Hippoglossinæ, the halibut group, the division nearest the cod-like stock from which the flounders are probably descended, the numbers range from 35 to 50. In the turbot group (Psettinæ) from 31 to 43." I have gradually arrived at the conclusion that Jordan's theory cannot be applied to the various groups which make up the suborder Acanthopterygii, and that the explanation of the fact that so many of its marine members agree in having 24 vertebræ is due to common descent from a Cretaceous marine type, probably Berycid, in which the number had been thus reduced. Further evolution would again have tended to an increase of the segments, especially in freshwater, deep-sea, and pelagic forms, for physiological requirements, which, however, are not always clearly apparent. The "natural selection" theory, by which Jordan has endeavoured to explain the variability in the number of vertebræ within restricted groups, can have no further claim than that of ingeniousness, since it implies a reversion of the evolutionlines that can be followed in the minor groups of the Pleuronectidae, especially the Hippoglossina and Soleinae.

Another good reason for regarding the Amphistiidæ and Zeidæ as related to the ancestral type of the Pleuronectidæ is the fact that the ventral fin of the latter, although always much reduced, contains frequently as many as six articulated rays, sometimes with the addition of a simple ray (*Hippoglossus*).

I therefore propose the establishment of a division of the suborder Acanthopterygii, under the name of Zeorhombi, to be defined as aberrant, strongly compressed Perciformes, with very short præcaudal region, modified in the direction of the flat-fishes, and characterized by the combination of an increased number (7 to 9) of ventral rays, with absence of hypural spine (by which Berycidæ are excluded), or by asymmetry of the skull in the forms in which the spine of the ventral fin has been lost.

This division embraces three families only :--

* 'Temperature and Vertebræ: a Study in Evolution' (Ithaca, 1893), p. 25.

A distinct spinous dorsal fin; anal spines detached	
from the soft portion; a ventral spine; gills	
three and a half, three slits between them	1. Zeidæ.
Dorsal and anal spines few, continuous with the	
soft rays; a ventral spine	2. Amphistiidæ.
No spines; cranium twisted in front, with the two	
orbits on one side; gills four, a slit behind the	
fourth	3. Pleuronectidæ.

According to our present information the three families can be traced back to the Upper Eccene. The common ancestors of the Zeidæ and Amphistiidæ will probably be found in the Upper Cretaceous associated with the Berycidæ, to which they will no doubt prove to be related *.

It is fair that I should add that the idea of deriving the Pleuronectids from some form similar to Zeus had occurred to Mr. E. W. L. Holt some years ago. He had been so struck by the asymmetry in the number and arrangement of the dorsal and anal bony plates in the young of the John Dory that he induced his friend Mr. L. W. Byrne to examine the matter on a large number of specimens between $2\frac{3}{4}$ and 5 inches in length, captured by Plymouth trawlers. This study, which I hope Mr. Byrne may soon publish, demonstrates the large proportion of specimens with an asymmetrical arrangement of the plates and the apparent tendency to vary especially in the direction of an asymmetry in which the plates of the right or of the left side predominate. It is a pity that so little should be known of the habits of the John Dory, in view of the suggestion put forth a few years ago by Verrill †, when dealing with the sleep of some Labridæ, first observed by Möbius f. "The common Tautog or Blackfish (Tautoga onitis)," says Verrill, " has the curious habit of resting upon one side, half buried among gravel, or partly under stones, and is often curved in strange positions. It is easy to imagine that the flounders originated from some symmetrical ancestral form that acquired, like the tautog, the habit of resting upon one side, at first only when sleeping, but afterwards continually, owing to the greater protection that this habit and its imitative coloration afforded. The one-sided coloration and the changes in the position of the eyes, etc., would gradually follow in accordance with wellknown laws of evolution,"

* On the ground of the number of ventral rays the Zeidæ have been brigaded with the Berycidæ by Woodward (Cat. Foss. Fish. iv. p. 384).

† Amer. Journ. Sci. (4) iii, 1897, p. 136.

‡ Zool. Garten, 1867, p. 148.

Mr. Byrne, who has seen Zeus alive at Plymouth, informs me that it does not live well in an aquarium and has not been observed to "sleep," but that it swims in a lop-sided fashion, at any rate in captivity, and also seems to use the soft dorsal and anal fins as organs of propulsion, moving them in waves, much as a needle-fish does.

XLIII.—A new Arrangement of the existing Species of Equidæ, with the Description of a new Subspecies of "Zebra." Ву R. I. Рососк.

It is customary to classify existing Equidæ as Horses, Asses, and Zebras.

The genus Equus, Linn. (Syst. Nat. ed. x. 1766), originally contained E. caballus (the domestic horse), E. asinus (the domestic ass), and E. zebra (the mountain zebra, with which Linneus included the quagga).

In 1825 Gray (Zool. Journ. i. p. 241) established the genus Asinus for E. vulgaris (=asinus), E. zebra, E. quagga, and E. Burchelli. In other words, he divided the Equide into "Horses" and "Asses."

Hamilton Smith went a step further, and removed from Gray's genus Asinus, under the name Hippotigris, H. zebra, H. quagga, H. Burchelli, and added H. antiquorum, leaving Asinus for the African and Asiatic species of wild ass (Nat. Libr., Mamm. i. pp. 350-351). This classification expresses in technical language the prevalent notion as to the affinities of the species included, although generic value has been seldom accorded to the three groups. It was adopted nevertheless by Trouessart in 1898 (Cat. Mamm. ii.), E. Grevyi and a number of subspecific forms of E. Burchelli being included under Hippotigris.

Zebra is no doubt a convenient vernacular term for the striped as opposed to the unstriped species of Equida; but its technical equivalent *Hippotigris*, in the broad sense used by Hamilton Smith and the still broader application given to it by Trouessart, cannot, I think, be maintained as symbolizing a natural unit.

There is a mass of evidence favouring the view that the ancestors of Equus were striped. In that case the stripes of "zebras" are a heritage from a common ancestor. To that extent only are they a sign of affinity between the species which possess them. They have been retained where the physical conditions required their retention for purposes of

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